Vision Research 49 (2009) 164–172

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

The effect of aging on the orientational selectivity of the human visual system

Stanley W. Govenlock [a], Christopher P. Taylor [a], Allison B. Sekuler [a,b,*], Patrick J. Bennett [a,b,*]

[a] Department of Psychology, Neuroscience, and Behaviour, McMaster University, Hamilton, Ontario, Canada L8S 4K1
[b] Centre for Vision Research, York University, Toronto, Ontario, Canada

ARTICLE INFO

Article history:
Received 2 October 2007
Received in revised form 3 October 2008

Keywords:
Aging
Orientation
Channels
Masking
Cortex
Psychophysics

ABSTRACT

Leventhal et al. (*Science*, 2003, 300(5620), 812–815) reported that orientation selectivity of V1 neurons was significantly reduced in older macaque monkeys, which suggests that mechanisms that encode orientation in humans may become more broadly tuned in old age. We examined this hypothesis in two experiments that used sine-wave masking and notched-noise masking to estimate the bandwidth of orientation-selective mechanisms in younger (age ≈ 23 years) and older (age ≈ 68 years) human adults. In both experiments, the orientation selectivity of masking was essentially identical in younger and older subjects.

1. Introduction

Many aspects of vision decline in old age (Sekuler & Sekuler, 2000). Some of the effects of aging can be attributed to changes in the optical quality of the eye (Weale, 1961), but optical changes alone cannot explain all of the age-related changes in vision (e.g., Bennett, Sekuler, & Ozin, 1999; Sekuler, Bennett, & Mamelak, 2000). Although non-sensory factors may affect performance in visual tasks, generally it is thought that impaired visual performance in older adults is due, at least in part, to changes in the anatomical or physiological characteristics of visual neurons (Bennett et al., 1999; Delahunt, Hardy, & Werner, 2008; Sekuler & Sekuler, 2000). Consistent with this view, Leventhal, Wang, Pu, Zhou, and Ma (2003) and Schmolesky, Wang, Pu, and Leventhal (2000) reported that senescent macaque V1 neurons are less selective for orientation than neurons in younger adult macaques. These physiological findings raise the possibility that mechanisms that encode orientation are degraded in older human adults.

Recently, Delahunt et al. (2008) investigated the tuning properties of orientation-selective mechanisms in younger and older adults by measuring detection thresholds for a Gabor pattern that was presented simultaneously with a sine-wave mask that varied in orientation. The shape of the masking functions were similar in both age groups, which suggests that the bandwidth of orientation-selective mechanisms does not change significantly with age. This psychophysical result differs significantly from the physiological reports, and therefore we thought it would be worthwhile to reexamine the issue of age differences in orientation selectivity in two masking experiments. Experiment 1 used a sine-wave mask like Delahunt et al. (2008). Experiment 2 used a notched-filtered noise mask.

2. Experiment 1: Sine-wave grating masking

Orientation tuning curves were obtained by measuring detection thresholds for a Gaussian-damped sine-wave grating embedded in a sine wave mask (Campbell & Kulikowski, 1966). The spatial frequency and contrast of the mask was fixed, but its orientation varied across conditions.

2.1. Methods

For all of the experiments reported here, the research protocol was approved by McMaster University's Research Ethics Board and informed consent was obtained from each subject prior to the start of the study.

2.1.1. Subjects

Twelve older and 12 younger paid subjects participated in the main experiment. An additional group of four younger subjects participated in a control experiment that measured the effect of reduced retinal illuminance on masking. All subjects completed vision and general health questionnaires to screen for visual

* Corresponding authors. Address: Department of Psychology, Neuroscience, and Behaviour, McMaster University, Hamilton, Ontario, Canada L8S 4K1.
E-mail addresses: govenlock@mcmaster.ca (S.W. Govenlock), sekuler@mcmaster.ca (A.B. Sekuler), bennett@mcmaster.ca (P.J. Bennett).

0042-6989/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2008.10.004

pathology, such as cataracts, macular degeneration, glaucoma, and amblyopia. Near and far decimal logMAR acuities were measured for all subjects with CSV-100EDTRS eye charts (Precision Vision, LaSalle, Illinois, USA). When measuring acuity, subjects wore their normal optical correction for each distance. Older subjects completed the Mini-Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975) to screen for age-related dementia. All older subjects scored within the normal range for their age groups on the MMSE (Crum, Anthony, Bassett, & Folstein, 1993). The means and standard deviations of age, near and far acuities, and MMSE scores are presented in Table 1. All subjects had normal or corrected-to-normal acuity and no known vision health problems (see Table 1 for details).

2.1.2. Stimuli and apparatus

The experiment was programmed in MatLab v5.2.1 (The Mathworks) using the Psychophysics and Video Toolboxes (Brainard, 1997; Pelli, 1997) running on an Apple G4 PowerMac computer. The stimuli were displayed on a 21-inch Apple Studio Display. Display size was 1024 × 768 pixels, which subtended visual angles of 19.1° horizontally and 14.4° vertically from the viewing distance of 114 cm. The frame rate was 75 Hz, noninterlaced. Calibration was done using a PhotoResearch PR-650 spectracolorimeter, and the calibration data were used to build a 1779-element look-up table (Tyler, Chan, Liu, McBride, & Kontsevich, 1992). When constructing the stimuli used on each trial, the computer software selected appropriate luminance values from the calibrated look-up table and stored them in the 8-bit look-up table of the display. Average luminance of the display was 32 cd/m^2 and was constant throughout the experiment. The monitor was the only source of light in the experimental room during testing. Viewing was binocular through natural pupils, and a chin/forehead rest was used to stabilize viewing position.

The visual target – 256 × 256 pixels, or 4.8 × 4.8°, in size – was a horizontal (0°), 2.9 *c/deg* sine-wave grating. Target contrast was modulated by a radially-symmetric Gaussian window ($2\sigma = 1.2°$). The spatial phase of the grating, relative to the center of the Gaussian window, was 0° (i.e., cosine phase). The target was masked by a 256 × 256 pixel sine-wave grating. Mask contrast was 0.2, and was modulated by a circular aperture (diameter = 256 pixels). The addition of the target to the sine-wave mask introduces a spatial pattern of beats which could be used to detect the target (Nachmias, 1993). To make it more difficult for subjects to learn to use a *specific* pattern of beats to detect the target, on each interval of every trial the phase of the mask was randomized and the spatial frequency of the mask was uniformly jittered ± 0.1 log units around the target frequency of 2.9 *c/deg*. In different conditions, the mask orientation was offset from the target's orientation by 0, ±15, ±30, ±45, ±60, ±75, or ±85°.

A separate control experiment was conducted to measure the effects of retinal illuminance on orientation masking. Four young subjects were each tested in two conditions. Stimuli in the High Luminance condition were the same as those described in the previous paragraphs. In the Low Luminance condition, subjects viewed the display through neutral density filters that reduced average luminance from 32 cd/m^2 to about 4 cd/m^2. This difference in stimulus luminance corresponds to a reduction of retinal illuminance of approximately 0.65 log units in young subjects (Betts, Sekuler, & Bennett, 2007), which is slightly larger than Weale's (Weale, 1961) estimate of the reduction in retinal illuminance that occurs between the ages of 20 and 60 years. The order of luminance conditions was counter-balanced across subjects.

2.1.3. Procedure

Thresholds were measured with a two-interval forced-choice (2-IFC) task. A circular (diameter = 6 pixels) high-contrast fixation spot was presented in the center of the display. After fixating on the spot, the subject began a trial by pressing the space bar on a standard computer keyboard. The fixation point then was erased, and, after a delay of 500 ms, followed by two successive stimulus intervals. The duration of each stimulus interval was 200 ms, and the inter-stimulus interval was 500 ms. Each stimulus interval contained a 1-pixel wide high-contrast circle (diameter = 256 pixels) that served to mark the spatial and temporal extent of the stimulus. One interval contained the target-plus-mask, the other contained the mask alone, and the subject's task was to select the interval that contained the target by pressing one of two response keys. An auditory tone provided feedback after incorrect responses; no sound followed a correct response. Subjects were informed that the probability of the target appearing in the first stimulus interval was 0.5.

Target contrast was varied across trials using QUEST (Watson & Pelli, 1983). The seven mask orientation conditions were intermixed, and the direction of the orientation offset (i.e., clockwise vs. counter-clockwise) was selected randomly on each interval of each trial. A session ended when each staircase had accumulated 45 trials.

2.2. Results

All statistical analyses were done with R (R Development Core Team, 2007). When appropriate, the Huynh–Feldt correction, $\tilde{\epsilon}$, was used to adjust the degrees-of-freedom to correct for violations of the sphericity assumption underlying F tests for within-subject variables (Maxwell & Delaney, 2004). In cases where the Huynh–Feldt correction is used, the reported p values are the adjusted p values. Effect size was expressed as Cohen's f (Cohen, 1988), and was calculated using formulae described by Kirk (1995). When $F < 1$, the effect size was assumed to be zero (see Kirk, 1995, page 180). Between-group t tests assumed unequal group variances and used the Welch–Satterthwaite formula to adjust the degrees-of-freedom: p values listed for such tests are the adjusted p values.

The psychometric function was defined as

$$p = 1 - (1 - \gamma)\exp\left(-10^{\beta\log_{10}(c/\alpha)}\right) \quad (1)$$

where p is proportion correct, γ is the guessing rate, c is stimulus contrast, β governs the slope of the psychometric function, and α corresponds to threshold (i.e., the stimulus contrast that yields a response accuracy of 81.6% correct). The guessing rate was set to 0.5,

Table 1
Age, acuity, and Mini-Mental State Exam (MMSE).

Experiment	Number of subjects	Age (μ, σ)	Near logMAR acuity (μ, σ)	Far logMAR acuity (μ, σ)	MMSE (μ, σ)
1	12 older	68.75 (4.18)	0.00 (0.12)	−0.04 (0.09)	29.08 (1.16)
	12 younger	23.67 (3.63)	−0.15 (0.07)	−0.10 (0.11)	
1 (control)	4 younger	22.5 (0.58)	−0.14 (0.04)	−0.18 (0.06)	
2	12 older	66.50 (3.58)	−0.02 (0.10)	−0.03 (0.09)	29.25 (1.22)
	12 younger	23.00 (3.72)	−0.15 (0.09)	−0.13 (0.08)	
2 (control)	5 younger	22.4 (0.56)	−0.14 (0.03)	−0.17 (0.06)	

and a maximum likelihood curve fitting procedure was used to estimate β and α for each subject in each condition.

One older subject in the main experiment had thresholds that were 3–3.4 standard deviations higher than the group mean when the mask orientation was 0, 15, and 30°. These thresholds were deemed outliers, and therefore thresholds from this subject were discarded prior to analyzing the data.

The grand mean of β was 3.5. An ANOVA on the log-transformed values of β found that the main effects of group, $F(1,21) = 1.60$, $f = 0.06$, $p = 0.22$, and mask orientation, $F(6,126) = 0.73$, $\tilde{\epsilon} = 0.91$, $p = 0.61$, as well as, the group x orientation interaction, $F(6,126) = 0.97$, $\tilde{\epsilon} = 0.91$, $p = 0.44$, were not significant. Hence, we did not find any evidence that the slope of the psychometric function varied systematically across conditions or groups.

Detection thresholds from the main experiment are presented in Fig. 1 as a function of mask orientation and age. Thresholds declined with increasing mask orientation in both age groups, but thresholds from older subjects reached a lower asymptote more quickly than thresholds from younger subjects. Consequently, the difference between groups increased slightly as mask orientation increased. An ANOVA on log-transformed thresholds found significant main effects of age, $F(1,21) = 20.21$, $f = 0.35$, $p = 0.0002$, and mask orientation, $F(6,126) = 162.44$, $f = 2.45$, $\tilde{\epsilon} = 0.86$, $p < 0.0001$, and a significant age x orientation interaction, $F(6,126) = 2.79$, $f = 0.26$, $\tilde{\epsilon} = 0.86$, $p = 0.019$.

Thresholds were fit with the equation

$$T(x) = k + a \cdot \exp\left(-\frac{x}{b}\right) \quad (2)$$

where T is threshold, x is the mask's orientation offset, k is the lower asymptote, a is the difference between the maximum and the lower asymptote, and b governs the rate of decline from the maximum threshold, $(k + a)$, to the minimum threshold, k. Eq. 2 was first fit to the average thresholds in each age group, and the resulting parameters were used to draw the smooth curves in Fig. 1; Eq. 2 provided reasonably good fits to the data in both age groups. Next, Eq. 2 was fit to the data from each subject. The means and standard errors of the best-fitting parameters are listed in Table 2. Separate t-tests found that the value of k differed significantly between age groups, $CI_{95\%} = (0.028,\ 0.014)$, $t(21) = 3.53$, $p = 0.003$, whereas a, $CI_{95\%} = (-0.013,\ 0.061)$, $t(21) = 1.35$, $p = 0.19$, and b, $CI_{95\%} = (-10.31, 5.45)$, $t(21) = -0.65$, $p = 0.52$, did not. The difference in k reflects the fact that the lower asymptote of the masking function was significantly higher in older subjects.

Table 2
Parameters k, a, b, and $\theta_{1/2}$ estimated in the sine-wave masking experiment.

	Younger subjects $\hat{\mu} \pm \hat{\sigma}_{\mu}$	Older subjects $\hat{\mu} \pm \hat{\sigma}_{\mu}$
k	1.43 ± 0.15 $(\times 10^{-2})$	2.82 ± 0.36 $(\times 10^{-2})$
a	0.90 ± 0.08 $(\times 10^{-1})$	1.14 ± 0.15 $(\times 10^{-1})$
b	16.79 ± 1.79	14.36 ± 3.25
$\theta_{1/2}$	14.41 ± 1.16	14.33 ± 3.09

Previous estimates of the orientation selectivity of masking often have been expressed in terms of half-amplitude half-bandwidth, $\theta_{1/2}$, defined as the mask orientation at which threshold drops to one-half of its peak value. Eq. 2 was used to estimate $\theta_{1/2}$ for each subject. The overall mean of $\theta_{1/2}$ was 14.4°, $CI_{95\%} = (11.1, 17.6)$. The difference between the group means, listed in Table 2, was not statistically significant, $CI_{95\%} = (7.23,\ 7.07)$, $t(21) = -0.024$, $p = 0.98$.

The grand mean of β measured in the control experiment was 3.6, and a 2 (luminance) $\times$ 7 (orientation) ANOVA on log-transformed values of β found no significant effects ($F \leqslant 1.93$, $f \leqslant 0.13$, $p \geqslant 0.26$ in all cases). Detection thresholds from the control experiment are shown in Fig. 2. Thresholds were higher in the low luminance condition at all mask orientations. A within-subjects ANOVA on log-transformed thresholds revealed significant main effects of luminance, $F(1,3) = 47.95$, $f = 0.92$, $p = 0.006$, and mask orientation, $F(6,18) = 76.71$, $f = 2.84$, $\tilde{\epsilon} = 0.30$, $p = 0.0001$. The interaction between luminance and orientation was not significant, $F(6,18) = 1.20$, $f = 0.15$, $\tilde{\epsilon} = 0.41$, $p = 0.364$, but a more focussed test of the linear trend of threshold across conditions did reveal a significant group $\times$ trend interaction, $F(1,3) = 11.83$, $f = 1.64$, $p = 0.041$. This interaction suggests that the slope of the masking function was shallower in the low luminance condition. Eq. 2 was fit to data from each subject in each luminance condition, and the best-fitting parameters, averaged across subjects, are shown in Table 3. Separate t tests found that k differed across lumi-

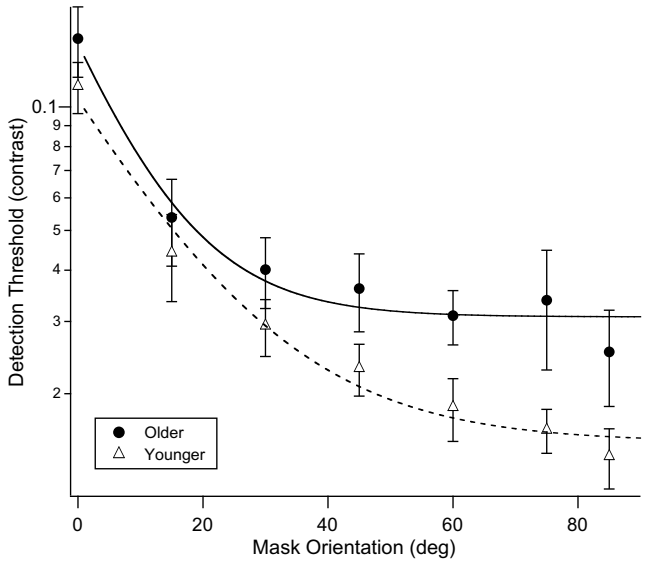

Fig. 1. Sine-wave masking data. Mean detection thresholds for older and younger subjects are plotted as a function of mask orientation. The orientation of the target grating was 0°. Error bars represent the 95% confidence interval of the mean. Eq. 2 was fit to the average thresholds from each age group. The solid and dashed curves represent the results for older and younger subjects, respectively.

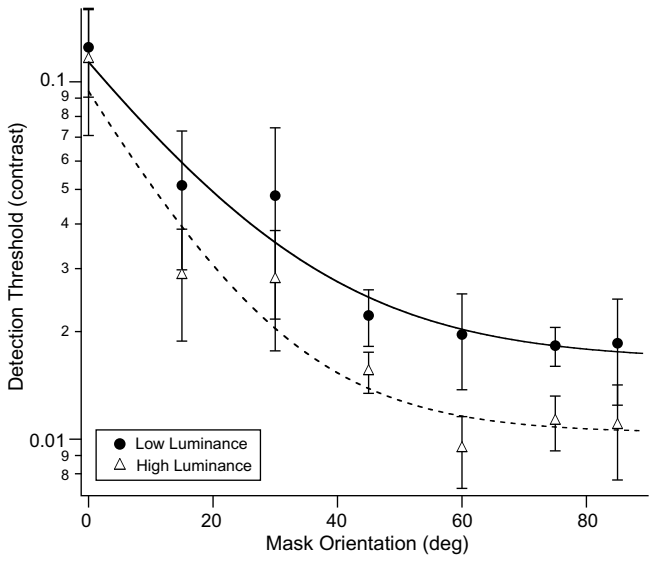

Fig. 2. Low luminance control experiment using a sine-wave mask. Mean detection thresholds measured at two average luminances for four younger subjects are plotted as a function of mask orientation. The orientation of the target grating was 0°. Error bars represent the 95% confidence interval of the mean. Eq. 2 was fit to the average thresholds in each condition. The solid and dashed curves represent the results for low and high luminance conditions, respectively.

Table 3
Parameters k, a, b, and $\theta_{1/2}$ estimated in the sine-wave masking control experiment.

	High luminance $\hat{\mu} \pm \hat{\sigma}_{\mu}$	Low luminance $\hat{\mu} \pm \hat{\sigma}_{\mu}$
k	1.08 ± 0.06 $(\times 10^{-2})$	1.68 ± 0.10 $(\times 10^{-2})$
a	1.02 ± 0.23 $(\times 10^{-1})$	1.03 ± 0.16 $(\times 10^{-1})$
b	12.62 ± 3.13	17.10 ± 2.11
$\theta_{1/2}$	10.43 ± 2.67	15.13 ± 1.92

nance levels, $CI_{95\%} = (-0.010, -0.002)$, $t(3) = -4.75$, $p = 0.017$, but that a, $CI_{95\%} = (-0.089, 0.086)$, $t(3) = -0.05$, $p = 0.959$, and b, $CI_{95\%} = (-13.96, 5.01)$, $t(3) = -1.50$, $p = 0.23$, did not. The masking bandwidth ($\theta_{1/2}$) also did not vary significantly between luminance conditions, $CI_{95\%} = (-12.83, 3.44)$, $t(3) = -1.84$, $p = 0.16$.

2.3. Discussion

Experiment 1 measured detection thresholds for a Gabor pattern embedded in a sine-wave mask whose orientation was variably offset from that of the target. As has been found previously, thresholds in both age groups were highest when the target and mask had the same orientation, and declined rapidly and significantly as the difference between orientations increased (Anderson, Burr, & Morrone, 1991; Blake & Holopigian, 1985; Campbell & Kulikowski, 1966; Delahunt et al., 2008; Phillips & Wilson, 1984). There was no evidence that the selectivity of orientation masking, as indexed by $\theta_{1/2}$, was broader in older results. In this regard, our results are consistent with the human behavioral findings of Delahunt et al. (2008), but differ from predictions based on single cell electrophysiology in macaques (Schmolesky et al., 2000; Leventhal et al., 2003).

Estimates of $\theta_{1/2}$ from a subset of conditions in several previous masking experiments are shown in Table 4. The values of $\theta_{1/2}$ listed for Anderson et al. (1991) and Phillips and Wilson (1984) were estimated directly from the published masking curves, and are not the bandwidths of the underlying orientation-selective mechanisms that the authors derived from the masking data. All of the studies listed in the table used a static sine wave target, but the spatial frequency of the target varied over a 10-fold range. The masks were all narrow-band in terms of spatial frequency, but differed in other ways: Phillips and Wilson (1984) used a static, high-contrast sine-wave grating; Campbell and Kulikowski (1966) used static high-contrast sine-wave gratings and narrow-band dynamic noise; Anderson et al. (1991) used a high-contrast sine-wave grating whose spatial phase was jittered randomly at 50 Hz; Delahunt et al. (2008) used a static sine-wave grating set to a contrast equal to two times detection threshold; Blake and Holopigian (1985) used a narrow-band dynamic noise that consisted of two orientations that were rotated symmetrically about the target's orientation. Despite these differences across experiments, the estimates of $\theta_{1/2}$ all fall within the range of 11–30°, and the mean value of 17.5° is only 3° greater than current estimate of $\theta_{1/2}$. Hence, our estimate of orientation masking bandwidth is similar to those reported previously.

Table 4
Estimates of $\theta_{1/2}$ derived from masking functions in several experiments.

Source	Target (c/°)	$\theta_{1/2}$ (°)
Campbell and Kulikowski (1966)	10	12
Phillips and Wilson (1984)	2	14.6
	8	16.4
Blake and Holopigian (1985)	1.25	30
	8	23
Anderson et al. (1991)	3	15.2
Delahunt et al. (2008)		
– Older & younger subjects	1 & 4	11.5
Mean value:		17.5

A high-contrast mask that is oriented orthogonally to a target grating can produce masking (Burbeck & Kelly, 1981; Burr & Morrone, 1987; Foley, 1994), and an increase in such masking in older subjects could explain why the lower asymptote of the masking function was higher in those subjects. To test this idea, we measured masking functions in five older and four younger subjects using the same methods as Experiment 1, except that a no-mask condition was added to the experimental conditions. For younger subjects, thresholds in the no-mask condition were ≈ 0.18 log units lower than thresholds measured with a ±85° mask. For older subjects, the threshold difference was ≈ 0.11 log units. Hence, there was no evidence that orthogonal masks produced greater masking in older subjects. The luminance control experiment found that reducing retinal illuminance in younger subjects raised k. It is likely, therefore, that age differences in retinal illuminance (Weale, 1961) contributed to the age differences in the asymptotic level of the masking functions.

3. Experiment 2: Notched-noise masking

Adding a Gabor target to a sine-wave mask that differs in orientation produces spatial beats. In Experiment 1, the spatial phase and frequency of the mask varied slightly across trials to make it difficult to detect the target based on the presence of a *particular* pattern of spatial beats. Nevertheless, subjects may have detected the target on the basis of the presence of spatial beats or other local spatial distortions in the mask (Nachmias, 1993). Experiment 2 minimized the possibility that subjects used such cues by measuring detection thresholds for a Gabor pattern embedded in static noise that was broadband in terms of spatial frequency. The spatial frequency selectivity of visual mechanisms has been estimated in experiments that used noise masks that were band-pass filtered (e.g., Stromeyer & Julesz, 1972) or low- and high-pass filtered (e.g., Henning, Hertz, & Hinton, 1981). This experiment used a

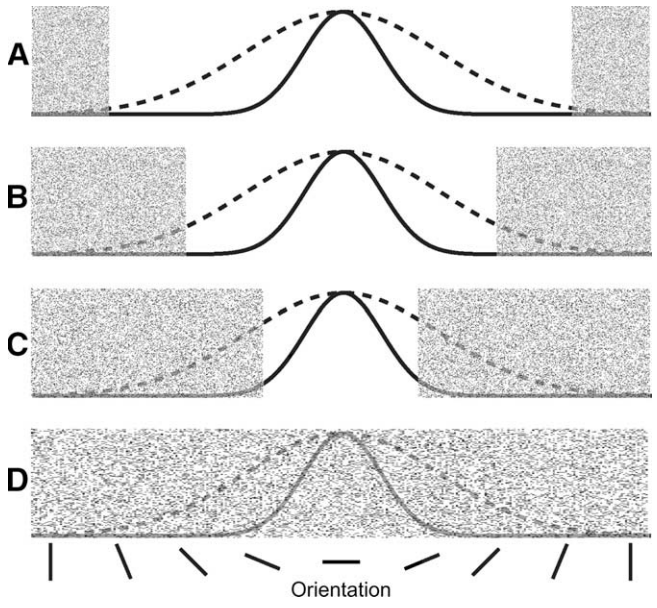

Fig. 3. Illustration of the notched-noise masking paradigm. The solid and dashed lines in each panel illustrate hypothetical orientation tuning functions that differ in bandwidth. The orientation content of the external noise is illustrated by the shaded regions. (A) Illustrates the orientation spectrum of a noise that has been filtered with a wide notch filter centered on the horizontal orientation. The notch width is progressively narrower in (B) and (C), and is zero in (D). Noise falling within the pass band of the orientation filters will increase response variability, and lower the signal-to-noise ratio. Notice that, in (B) and (C), more noise falls within the pass band of the broader orientation filter.

notch filter to vary the orientation content of a noise mask: the notch was centered on the target's orientation, and the width of the notch varied across conditions (see Fig. 3). Notched-noise has been used to investigate contrast discrimination (Henning & Wichmann, 2007), the frequency selectivity of auditory channels (e.g., Patterson, 1976), the spatial frequency tuning of luminance and chromatic visual mechanisms (Losada & Mullen, 1995; Mullen & Losada, 1999), and the orientation tuning of binocular (i.e., cyclopean) mechanisms (Hibbard, 2005). In this experiment the notched-noise method was used to compare the orientation selectivity of masking in younger and older subjects.

3.1. Methods

3.1.1. Subjects

Twelve older and 12 younger subjects were paid for participating in this experiment. An additional group of five younger subjects participated in a control experiment that measured the effect of reduced retinal illuminance on masking. The subjects were screened with the same protocol used in Experiment 1. The ages, acuities, and MMSE scores for these subjects are listed in Table 1. As before, all older subjects scored within the normal range for their age groups on the MMSE (Crum et al., 1993). All subjects had normal or corrected-to-normal acuity and no known vision health problems (see Table 1 for details).

3.1.2. Stimuli and apparatus

The experimental apparatus was the same as in Experiment 1.

The visual target was a horizontally-oriented (i.e., 0°) 2.9 *c/deg* Gabor pattern with the same parameters as in Experiment 1. Two-dimensional static noise fields (256 × 256 pixels in size) were constructed by digitally filtering white Gaussian noise. Prior to filtering, the value of each noise pixel was drawn randomly from a Gaussian distribution with a mean of 0 and a variance of 0.16. Noise values beyond ±2 standard deviations from the mean were discarded and replaced by random samples from the remaining contrast values.

Orientation filtering was done in the Fourier domain using Matlab's `fft2` function and custom software. In different conditions, the filtering procedure removed all Fourier components within ±15, ±30, ±45, ±60, ±75, and ±80° of the target orientation. In addition, there was one condition in which no orientation filtering was performed. Thus, the filtering can be thought of as notch filtering along the orientation dimension, with the notch centered on 0° and seven notch widths ranging from 0 to 160°. We did not include a no-mask condition because pilot experiments showed that such thresholds are very similar to thresholds measured with a notch width of 160°. A unique noise field was constructed for each interval of every trial. Noise contrast was modulated by a circular window (diameter = 256 pixels). Example stimuli are shown in Fig. 4.

A separate control experiment was conducted to measure the effects of retinal illuminance. Five young subjects were each tested in High and Low Luminance conditions. Stimuli in the High Luminance condition were the same as those described in the previous paragraphs. In the Low Luminance condition, subjects viewed the display through neutral density filters that reduced average luminance from 32 cd/m^2 to about 4 cd/m^2. The order of luminance conditions was counter-balanced across subjects.

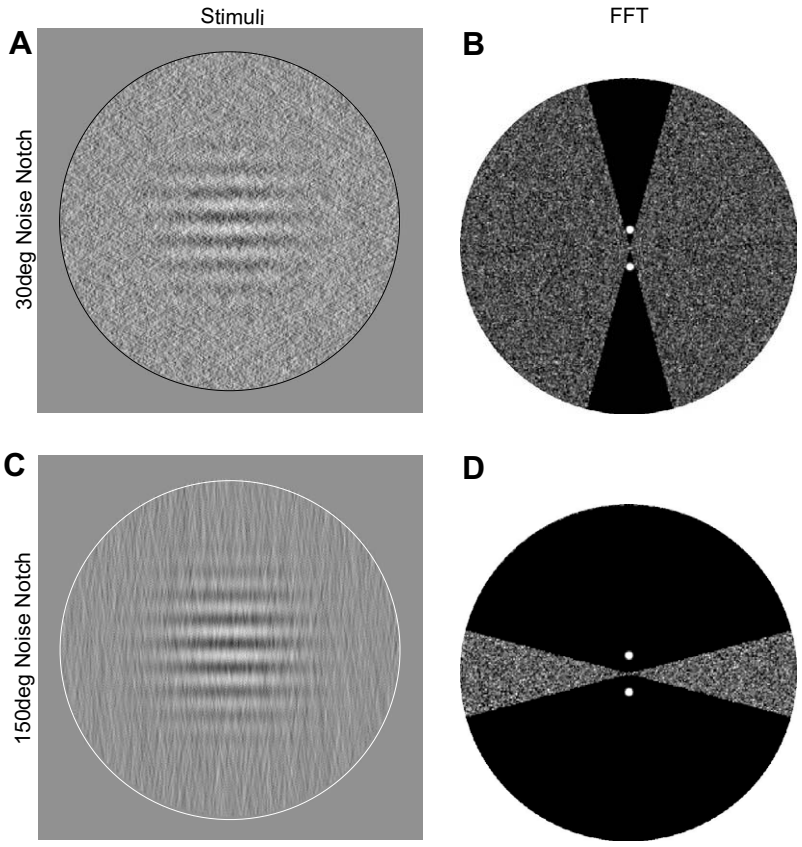

Fig. 4. Example of the stimuli used in the notched-noise masking experiment. (A) The target is shown at supra-threshold contrast embedded in noise having only a small orientation notch (30°). (B) The Fourier transform of the stimulus in (A). Orientation is represented on the angular axis, and spatial frequency is represented by distance from the origin. The two bright points are the frequency components of the target. Note that, in this type of plot, a horizontal grating is represented by two vertically-aligned points, whereas a vertical grating would be represented as two horizontally-aligned points. The broadband noise mask contains non-zero amplitudes at all frequency components except those falling within 30° of the target's orientation. (C) and (D) show an example of a stimulus constructed with a notch bandwidth of 150°.

3.1.3. Procedure

The same 2-IFC task that was employed in Experiment 1 was used here. Target contrast was varied across trials using QUEST. Staircases from all seven notch noise conditions were intermixed randomly, and a session ended when each staircase had accumulated 45 trials.

3.2. Results

A maximum likelihood curve fitting procedure was used to estimate β and α (Eq. 1) for each subject in each condition. Threshold was defined as α (i.e., the contrast needed to produce a correct response rate of 81.6%). One subject in the younger group had thresholds that were, on average, more than five standard deviations higher than the mean thresholds from the other young subjects. This subject was declared an outlier and was not used in subsequent statistical analyses.

The mean value of β was 3.8, which was similar to the value obtained in Experiment 1. However, unlike what was found in Experiment 1, an ANOVA on log-transformed values of β found that the main effect of mask orientation was significant, $F(6,136) = 3.26$, $f = 0.33$, $\tilde{\epsilon} = 0.90$, $p = 0.007$. This main effect reflected the fact that β was higher when the noise notch width was 60 and 90° ($M = 4.7$) than in the other conditions (M = 3.5). This result means that the shapes of the masking curves will not be invariant with changes in the threshold criterion. This point is elaborated in the Discussion. Importantly, however, the slope of the psychometric function did not vary across groups: Both the main effect of group, $F(1,21) = 1.84$, $f = 0.08$, $p = 0.19$, as well as the group × orientation interaction, $F(6,126) = 0.47$, $\tilde{\epsilon} = 0.90$, $p = 0.81$, were not significant. Therefore, the magnitude of any observed group differences in threshold do not depend on the threshold criterion.

Detection thresholds varied significantly with notch bandwidth, but were similar in the two age groups (Fig. 5). An ANOVA on log-transformed thresholds found that the main effect of notch bandwidth was significant, $F(6,126) = 189.89$, $f = 2.65$, $\tilde{\epsilon} = 0.88$, $p < 0.0001$, but that the main effect of age, $F(1,21) = 0.18$, $p = 0.67$, and the age × notch bandwidth interaction, $F(6,126) = 2.12$, $f = 0.20$, $\tilde{\epsilon} = 0.88$, $p = 0.065$, were not. Although the overall interaction between age and notch bandwidth was not significant, a more focussed statistical test did find that the linear effect of notch bandwidth was smaller in older subjects, $F(1,21) = 4.12$, $f = 0.14$, $p = 0.05$. This age × linear trend interaction is due primarily to the fact that thresholds in the widest notch conditions were higher in older subjects.

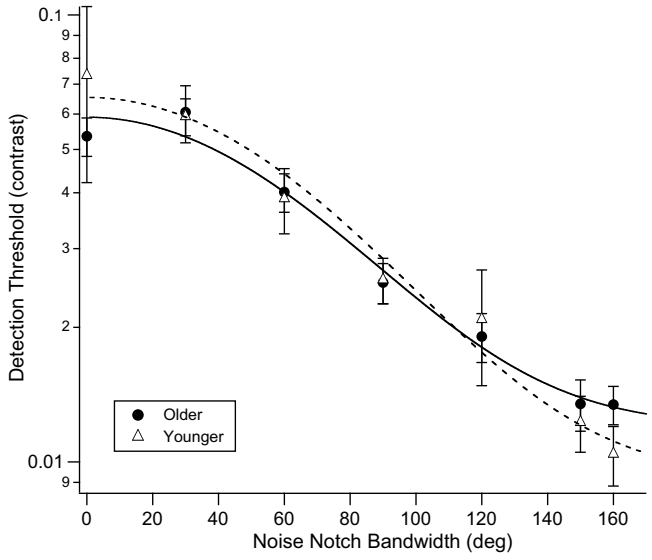

Fig. 5. Notched-noise masking. Mean detection thresholds for older and younger subjects plotted as a function of the full width of the orientation notch bandwidth. The notch was centered on the orientation of the target grating (i.e, 0°). Error bars represent the 95% confidence interval of the mean. Eq. 3 was fit to the average thresholds from each age group. The solid and dashed curves represent the results for older and younger subjects, respectively.

Preliminary analyses indicated that Eq. 2 provided a poor fit to the data from the current experiment. A much better fit was provided by the function

$$T(x) = k + a \cdot \exp\left(-\left(\frac{0.5x}{b}\right)^2\right) \quad (3)$$

where T is threshold, x is the full width of the noise notch, k is the lower asymptote, a is the difference between the maximum value and k, and b governs the rate of decline from the maximum, $(k + a)$, to the minimum, k. Eq. 3 was first fit to average thresholds in each age group by adjusting the values of k, a, and b to minimize the sum of the squared log differences between the observed and predicted thresholds across conditions. The resulting parameters were used to draw the smooth curves in Fig. 5, which fit the data in both age groups reasonably well. Next, Eq. 3 was fit to the data from each subject. The value of b for one subject was more than two standard deviations below the mean, and therefore was declared an outlier and not included in subsequent analyses. The means and standard errors of the best-fitting parameters are listed in Table 5. Separate t tests indicated that none of the parameters differed significantly across age (k: $CI_{95\%} = (-0.0002, 0.0055)$, $t(21) = 1.94$, $p = 0.069$; a: $CI_{95\%} = (-0.015, 0.006)$, $t(21) = -0.9$, $p = 0.38$; b: $CI_{95\%} = (-8.60, 10.33)$, $t(20) = 0.19$, $p = 0.85$). The statistical test on b remained non-significant when the outlier was included.

For each subject, the best-fitting version of Equation 3 was used to estimate $\theta_{1/2}$, which was defined as *one-half* of the notch width at which threshold fell to half of the maximum threshold. We used one-half of the notch width, rather than the full width, to enable comparisons between $\theta_{1/2}$ in the current Experiment with the values calculated in Experiment 1. The overall mean of $\theta_{1/2}$ was 42.2°, $CI_{95\%} = (38.1, 46.4)$; the mean value for each age group is listed in Table 5. The difference between age groups was not statistically significant, $CI_{95\%} = (-5.27, 11.04)$, $t(20) = 0.74$, $p = 0.47$.

The grand mean of β measured in the low luminance control experiment was 3.5. Interestingly, a 2 (luminance) × 7(orientation) ANOVA on log-transformed values of β found no significant effects (luminance: $F(1,4) = 0.08$, $p = 0.78$; notch width: $F(6,24) = 0.69$, $\tilde{\epsilon} = 1$, $p = 0.66$; luminance × notch width: $F(6,24) = 1.92$, $f = 0.28$, $\tilde{\epsilon} = 1$, $p = 0.12$). Hence, unlike what was found in the main experiment, there was no evidence that β varied systematically across conditions. Thresholds obtained in the control experiment are shown in Fig. 6. A within-subjects ANOVA performed on log-transformed thresholds found that the main effect of luminance was not significant, $F(1,4) = 6.13$, $f = 0.27$, $p = 0.7$, but that the main effect of notch bandwidth, $F(6,24) = 84.6$, $f = 2.67$, $\tilde{\epsilon} = 1$, $p < 0.0001$, and the luminance × notch bandwidth interaction, $F(6,24) = 9.75$, $f = 0.87$, $\tilde{\epsilon} = 1$, $p < 0.0001$, were significant.

Table 5
Parameters k, a, b, and $\theta_{1/2}$ estimated in the notched-noise masking experiment.

	Younger subjects $\hat{\mu} \pm \hat{\sigma}_{\mu}$	Older subjects $\hat{\mu} \pm \hat{\sigma}_{\mu}$
k	0.96 ± 0.19 ($\times 10^{-2}$)	1.06 ± 0.08 ($\times 10^{-2}$)
a	0.67 ± 0.14 ($\times 10^{-1}$)	0.49 ± 0.31 ($\times 10^{-1}$)
b	43.70 ± 3.16	44.56 ± 3.25
$\theta_{1/2}$	40.62 ± 2.43	43.51 ± 3.06

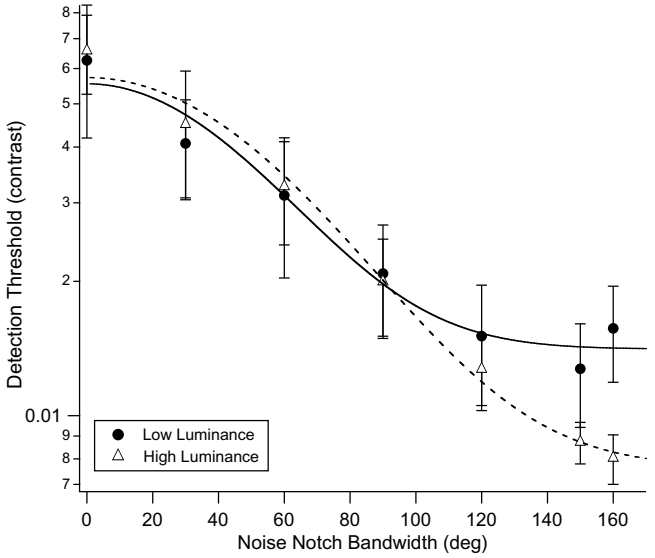

Fig. 6. Low luminance control experiment using notched-noise masking. Mean detection thresholds measured at two average luminances for five younger subjects are plotted as a function of the full notch bandwidth. The notch was centered on the orientation of the target grating (i.e., 0°). Error bars represent the 95% confidence interval of the mean. Eq. 3 was fit to the average thresholds in each condition; the solid and dashed curves represent the results for low and high luminance conditions, respectively.

Eq. 3 provided reasonably good fits to the average thresholds in each luminance condition (Fig. 6) as well as to the individual sets of data. The means and standard errors of the best-fitting parameters are shown in Table 6. Separate t tests indicated that k was significantly lower in the high luminance condition, $CI_{95\%} = (-0.010, -0.002)$, $t(4) = -4.32$, $p = 0.012$; b was significantly higher in the high luminance condition, $CI_{95\%} = (3.11, 7.43)$, $t(4) = 6.78$, $p = 0.002$; and a did not differ between luminance conditions, $CI_{95\%} = (-0.011, 0.026)$, $t(4) = 1.16$, p = 0.31. The bandwidth of orientation masking, $\theta_{1/2}$, was 35.19 and 34.97° in the high and low luminance conditions, respectively, a difference that was not statistically significant, $CI_{95\%} = (-4.85, 5.29)$, $t(4) = 0.12$, $p = 0.91$.

3.3. Discussion

Experiment 2 measured thresholds for a Gabor pattern embedded in notched-filtered noise to reduce the possibility that subjects could detect the target on the basis of spatial beats or other local spatial distortions in the mask. We found that thresholds in most conditions were very similar in older and younger subjects, and that the parameters of the masking function (Eq. 3) did not differ across age groups (Table 5). A test for linear trend suggested that threshold declined more slowly in older subjects than in younger subjects with increasing notch width. The results of the luminance control experiment, however, suggest that this slight difference in the shape of the masking function may simply be due to age differences in retinal illuminance. The key result for the present investigation, however, is the fact that there was no evidence for reduced orientation selectivity of masking in older subjects. In this regard, the results of the current experiment are similar to the behavioral results obtained in Experiment 1 and by Delahunt et al. (2008), but, again, are inconsistent with results from single cell electrophysiology (Schmolesky et al., 2000; Leventhal et al., 2003).

Table 6
Parameters k, a, b, and $\theta_{1/2}$ estimated in the notched-noise luminance control experiment.

	High luminance $\hat{\mu} \pm \hat{\sigma}_{\mu}$	Low luminance $\hat{\mu} \pm \hat{\sigma}_{\mu}$
k	0.75 ± 0.02 ($\times 10^{-2}$)	1.38 ± 0.15 ($\times 10^{-2}$)
a	0.50 ± 0.06 ($\times 10^{-1}$)	0.42 ± 0.07 ($\times 10^{-1}$)
b	37.80 ± 2.36	35.52 ± 2.96
$\theta_{1/2}$	35.19 ± 2.22	34.97 ± 3.87

In the main experiment, the slope of the psychometric function was higher in conditions that used notch widths of 60 and 90°. This difference in slope means that the shape of the masking function would change if a different threshold criterion (e.g., 70% correct) were used. However, such changes in the function's shape would be small. For example, defining threshold as the 70% correct point on the psychometric function (Eq. 1) would lower threshold by 0.097 log units if $\beta = 3$, and by 0.053 log units if $\beta = 5.5$. In other words, if the slopes in two conditions were 3 and 5.5, then changing the definition of threshold from 81.6% to 70% correct would introduce a *relative* change in threshold equal to $0.097 - 0.053 = 0.044$ log units or $\approx 10\%$. Smaller changes in the threshold criterion (e.g., from 81.6% to 75% correct) would produce smaller relative changes in threshold across conditions. In our experiment, β ranged from approximately 3–5.5, so using a different criterion for threshold would have only minor effects on the shape of the masking function. Therefore, variation of β across conditions cannot account for the finding that the masking function was much broader in Experiment 2 than Experiment 1. This point is reinforced by the fact that broad masking functions were obtained in the notched-noise luminance control experiment even though β did not vary significantly across conditions.

Our estimate of $\theta_{1/2}$ from Experiment 2 (42°) is similar to the value of 45° reported by Tootell et al. (1998) in an fMRI analysis of orientation tuning in V1 in humans. Of all the values listed in Table 4, our estimate of $\theta_{1/2}$ is closest to the value of 30° reported by Blake and Holopigian (1985), who used a two-component noise mask, but it is considerably larger than the other values in Table 4 as well as the estimate obtained in Experiment 1. It is not clear why $\theta_{1/2}$ was so much larger in Experiment 2. One possibility is that the broader orientation bandwidth was the result of using a noise mask that eliminated spatial beats as a potential cue for detecting the target. Such cues have been shown to be important for detecting and discriminating supra-threshold spatial patterns in several contexts, including masking experiments (Badcock, 1988; Derrington & Badcock, 1986; Hess & Pointer, 1987; Nachmias, 1993). In Experiment 1, such cues may have made it easier to detect the target in conditions where the orientations of the target and mask differed, and therefore decreased $\theta_{1/2}$. A related idea, suggested by a reviewer, is that the narrower masking functions obtained in Experiment 1 were due to the way beats and local distortions affected spatial probability summation (see Baker & Meese, 2007, p. 3102) .

Another possibility is that the value of $\theta_{1/2}$ obtained with sine-wave masks is unusually low because of the effects of off-channel looking (Blake & Holopigian, 1985; Henning & Wichmann, 2007; Henning et al., 1981; Patterson & Nimmo-Smith, 1980; Solomon & Pelli, 1994). If a subject can detect a target by monitoring one of several channels tuned to different orientations, then an efficient strategy would be to monitor the channel with the highest signal-to-noise ratio. In Experiment 1, the mask was asymmetrical: it consisted of a single orientation rotated clockwise or counter-clockwise relative to the target. Therefore, off-channel looking would enable a subject to minimize the effects of the mask by monitoring the responses of channels that responded best to orientations that differed from the target orientation, and therefore lead to narrower estimates of $\theta_{1/2}$. If the mask was rotated counter-clockwise relative to the target, for example, then the signal-to-noise ratio would be highest in a channel tuned to an

orientation that is clockwise relative to the target. Off-channel looking would not produce any benefit in Experiment 2 because the noise contained orientations that were placed symmetrically about the target's orientation. Hence, off-channel looking would produce smaller values of $\theta_{1/2}$ in Experiment 1 than in Experiment 2.

Blake and Holopigian (1985) estimated the effects of off-channel looking on the bandwidth of orientation masking by measuring masking with one- and two-component masks in a single subject, and found that $\theta_{1/2}$ was 6° larger when the mask contained two components oriented symmetrically about the target. So Blake and Holopigian (1985) obtained evidence that off-channel looking occurred, but the effect probably is too small to account for the difference between $\theta_{1/2}$ obtained in Experiments 1 and 2. On the other hand, Derrington and Henning (1989) found that the masking produced by a plaid pattern – composed of two sine-wave gratings oriented symmetrically about the target grating – was much greater than the sum of the component masking effects (also see Meese, Holmes, & Challinor, 2007; Ross & Speed, 1991). Moreover, Derrington and Henning (1989) obtained significant masking with plaids composed of orientations that differed significantly from the target's orientation (e.g., ±45 and ±67°). At least under some conditions, therefore, the orientation bandwidth of masking is greatly increased when the mask is a plaid rather than a sine-wave grating. The same mechanism that produces this excess masking with plaids – be it off-channel looking or some other non-linearity – may have contributed to the broader pattern of masking found in Experiment 2. The current results suggests that these mechanisms operate similarly in older and younger subjects.

4. General discussion

Orientation selectivity is reduced significantly in V1 cells in senescent cats (Hua et al., 2006) and monkeys (Schmolesky et al., 2000), but there is little evidence that the perception of orientation is impaired by normal aging. Betts et al. (2007) reported that sensitivity to orientation differences was reduced in older subjects when stimulus contrast was low, but not when stimulus contrast was high. Although Delahunt et al. (2008) found age differences in orientation discrimination thresholds at all stimulus contrasts, they attributed this effect to age differences in contrast sensitivity, rather than to orientation discrimination *per se*: When stimulus contrast was expressed in terms of multiples of detection threshold, orientation discrimination thresholds in older and younger subjects did not differ. In addition, Delahunt et al. reported that the orientational selectivity of sine-wave masking did not differ across age groups. Experiment 1 replicated Delahunt et al's finding: $\theta_{1/2}$ was approximately 14° in both age groups. The bandwidth of masking was considerably broader in Experiment 2 ($\theta_{1/2} \approx 42$ deg), but, again, did not differ in older and younger subjects. These findings suggest that orientation tuning may be preserved across the life span.

What might account for the apparent discrepancy between the physiological studies of the effects of aging on orientation coding (Hua et al., 2006; Schmolesky et al., 2000) and the psychophysical results reported here and elsewhere (Betts et al., 2007; Delahunt et al., 2008)? One possible explanation for the difference is that the physiological effects are caused by age differences in the effects of anesthesia, rather than visual processing *per se*. Evidence against this explanation comes from Wang, Zhou, Ma, and Leventhal (2005), who found that large variations in the level of anesthetic did not significantly alter the age differences in the physiological responses of V1 and V2 neurons. Another possibility is that older human subjects in our experiments, but not the anesthetized monkeys in the physiological studies, were able to use focussed attention to compensate for age-related physiological changes in V1 neurons. In monkeys, focussed attention alters the response properties of single neurons in many visual cortical areas (Maunsel, 2003); in humans, attention modulates the steady-state visually-evoked potential (ss-VEP; Di Russo & Spinelli, 1999) and the BOLD response in V1 (Smith, Cotillon-Williams, & Williams, 2006). Thus, it is plausible to suggest that visual attention may have boosted the signal-to-noise ratio of orientation-selective mechanisms in our older subjects, or perhaps allowed older subjects to use different functional neural networks for extracting the signal from visual neurons, as has been shown for a spatial frequency discrimination task (Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001; Della-Maggiore et al., 2000; McIntosh et al., 1999). However, there is as yet little evidence that attention significantly alters the tuning of cortical neurons, and at least one study has found that attention has no effect on orientation selectivity in V4 neurons (McAdams & Maunsel, 1999). Hence, the effect of attention on orientation selectivity remains unclear.

Another way of reconciling the physiological and psychophysical results is to consider which subset of cortical neurons might contribute to behaviour. The physiological difference in orientation selectivity between cells in young and old animals reflects the difference between *average* cells. However, a small number of cells in older cats (Hua et al., 2006) and monkeys (Schmolesky et al., 2000) remained highly selective for orientation. If psychophysical orientation judgments were most closely related to the responses of this relatively small group of highly-selective cells (Parker & Newsome, 1998), then we would not expect to find large age differences in orientation bandwidth. One way of testing this idea would be to use the steady-state visually evoked potential (ss-VEP) to measure orientation tuning (Regan & Regan, 1987). Because ss-VEP represents the average response of a large population of neurons, rather than just the most selective neurons, it might be more sensitive than psychophysical methods to age-related changes in the average orientation bandwidth of cortical mechanisms.

Acknowledgments

This research was supported by a grant from the Canadian Institutes of Health Research to P.J. Bennett and A.B. Sekuler, and by NSERC-PGS and CIHR-STIHR awards to S.W. Govenlock. Portions of this work were presented at the annual meeting of the Vision Sciences Society (Sarasota, FL USA, May 2006). The authors would like to thank Donna Waxman for her help with collecting the data.

References

Anderson, S. J., Burr, D. C., & Morrone, M. C. (1991). Two-dimensional spatial and spatial-frequency selectivity of motion-sensitive mechanisms in human vision. *Journal of the Optical Society of America. A, Optics, Image science, and Vision, 8*, 1340–1351.

Badcock, D. R. (1988). Discrimination of spatial phase changes: contrast and position codes. *Spatial Vision, 3*, 305–322.

Baker, D. H., & Meese, T. S. (2007). Binocular contrast interactions: Dichoptic masking is not a single process. *Vision Research, 47*, 3096–3107.

Bennett, P. J., Sekuler, A. B., McIntosh, A. R., & Della-Maggiore, V. (2001). The effects of aging on visual memory: Evidence for functional reorganization of cortical networks. *Acta Psychologica, 107*, 249–273.

Bennett, P. J., Sekuler, A. B., & Ozin, L. (1999). Effects of aging on calculation efficiency and equivalent noise. *Journal of the Optical Society of America. A, Optics, Image science, and Vision, 16*, 654–658.

Betts, L. R., Sekuler, A. B., & Bennett, P. J. (2007). The effects of aging on orientation discrimination. *Vision Research, 47*, 1769–1780.

Blake, R., & Holopigian, K. (1985). Orientation selectivity in cats and humans assessed by masking. *Vision Research, 25*, 1459–1467.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 443–446.

Burbeck, C. A., & Kelly, D. H. (1981). Contrast gain measurements and the transient/sustained. *Journal of the Optical Society of America, 71*, 1335–1342.
Burr, D. C., & Morrone, M. C. (1987). Inhibitory interactions in the human vision system revealed in pattern-evoked potentials. *Journal of Physiology, 389*, 1–21.
Campbell, F. W., & Kulikowski, J. J. (1966). Orientational selectivity of the human visual system. *Journal of Physiology, 187*, 437–445.
Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: Erlbaum Associates.
Crum, R. M., Anthony, J. C., Bassett, S. S., & Folstein, M. F. (1993). Population-based norms for the Mini-Mental state examination by age and education level. *Journal of the American Medical Association, 269*, 2386–2391.
Delahunt, P., Hardy, J., & Werner, J. (2008). The effect of senescence on orientation discrimination and mechanism tuning. *Journal of Vision, 8*, 1–9.
Della-Maggiore, V., Sekuler, A. B., Grady, C. L., Bennett, P. J., Sekuler, R., & McIntosh, A. R. (2000). Corticolimbic interactions associated with performance on a short-term memory task are modified by age. *Journal of Neuroscience, 20*, 8410–8416.
Derrington, A. M., & Badcock, D. R. (1986). Detection of spatial beats: Non-linearity or contrast increment detection? *Vision Research, 26*, 343–348.
Derrington, A. M., & Henning, G. B. (1989). Some observations on the masking effects of two-dimensional stimuli. *Vision Research, 29*, 241–246.
Di Russo, F., & Spinelli, D. (1999). Electrophysiological evidence for an early attentional mechanism in visual processing in humans. *Vision Research, 39*, 2975–2985.
Foley, J. M. (1994). Human luminance pattern-vision mechanisms: masking experiments require a new model. *Journal of the Optical Society of America. A, Optics, Image science, and Vision, 11*, 1710–1719.
Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). Mini-Mental state a practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research, 12*, 189–198.
Henning, G. B., Hertz, B. G., & Hinton, J. L. (1981). Effects of different hypothetical detection mechanisms on the shape of spatial-frequency filters inferred from masking experiments: I. noise masks. *Journal of the Optical Society of America, 71*, 574–581.
Henning, G. B., & Wichmann, F. A. (2007). Some observations on the pedestal effect. *Journal of Vision, 7*, 3.
Hess, R. F., & Pointer, J. S. (1987). Evidence for spatially local computations underlying discrimination of periodic patterns in fovea and periphery. *Vision Research, 27*, 1343–1360.
Hibbard, P. (2005). The orientation bandwidth of cyclopean channels. *Vision Research, 45*, 2780–2785.
Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., & Leventhal, A. G. (2006). Functional degradation of visual cortical cells in old cats. *Neurobiology of Aging, 27*, 155–162.
Kirk, R. E. (1995). *Experimental design: Procedures for the behavioral sciences* (3rd ed.). CA: Brooks/Cole, Pacific Grove.
Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science, 300*, 812–815.
Losada, M. A., & Mullen, K. T. (1995). Color and luminance spatial tuning estimated by noise masking in the absense of off-frequency looking. *Journal of the Optical Society of America. A, Optics, Image science, and Vision, 12*, 250–260.
Maunsel, J. (2003). The role of attention in visual cerebral cortex. In L. Chalupa & J. Werner (Eds.). *The visual neurosciences* (Vol. 2, pp. 1538–1545). Cambridge, MA: MIT Press.
Maxwell, S., & Delaney, H. (2004). *Designing experiments and analyzing data: A model comparison approach* (2nd ed.). Mahwah, New Jersey: Lawrence Erlbaum Associates.
McAdams, C., & Maunsel, J. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience, 19*, 431–441.
McIntosh, A. R., Sekuler, A. B., Penpeci, C., Rajah, M. N., Grady, C. L., Sekuler, R., et al. (1999). Recruitment of unique neural systems to support visual memory in normal aging. *Current Biology, 9*, 1275–1278.
Meese, T. S., Holmes, D. J., & Challinor, K. L. (2007). Remote facilitation in the fourier domain. *Vision Research, 47*, 1112–1119.
Mullen, K. T., & Losada, M. A. (1999). The spatial tuning of color and luminance peripheral vision measured with notch filtered noise masking. *Vision Research, 39*, 721–731.
Nachmias, J. (1993). Masked detection of gratings: The standard model revisited. *Vision Research, 33*, 1359–1365.
Parker, A. J., & Newsome, W. T. (1998). Sense and the single neuron: Probing the physiology of perception. *Annual Review of Neuroscience, 21*, 227–277.
Patterson, R. D. (1976). Auditory filter shapes derived with noise stimuli. *Journal of the Acoustical Society of America, 59*, 640–654.
Patterson, R. D., & Nimmo-Smith, I. (1980). Off-frequency listening and auditory-filter asymmetry. *Journal of the Acoustical Society of America, 67*, 229–245.
Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442.
Phillips, G., & Wilson, H. (1984). Orientation bandwidths of spatial mechanisms measured by masking. *Journal of the Optical Society of America. A, Optics, Image science, and Vision, 1*, 226–232.
R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.
Regan, D., & Regan, M. P. (1987). Nonlinearity in human visual responses to two-dimensional patterns, and a limitation of fourier methods. *Vision Research, 27*, 2181–2183.
Ross, J., & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society B: Biological Sciences, 246*, 61–69.
Schmolesky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience, 3*, 384–390.
Sekuler, A. B., Bennett, P. J., & Mamelak, M. (2000). Effects of aging on the useful field of view. *Experimental Aging Research, 26*, 103–120.
Sekuler, R., & Sekuler, A. B. (2000). Visual perception and cognition. In J. G. Evans, T. F. Williams, B. L. Beattie, J. P. Michel, & G. K. Wilcock (Eds.), *Oxford textbook of geriatric medicine* (pp. 874–880). New York: Oxford University Press.
Smith, A., Cotillon-Williams, N., & Williams, A. (2006). Attentional modulation in the human striate cortex: The time-course of the bold response and its implications. *Neuroimage, 29*, 328–334.
Solomon, J. A., & Pelli, D. G. (1994). The visual filter mediating letter identification. *Nature, 369*, 395–397.
Stromeyer, C. F. r., & Julesz, B. (1972). Spatial-frequency masking in vision: Critical bands and spread of masking. *Journal of the Optical Society of America, 62*, 1221–1232.
Tootell, R., Hadjikhani, N., Vanduffel, W., Liu, A., Mendola, J., Sereno, M., et al. (1998). Functional analysis of primary visual cortex (v1) in humans. *Proceedings of the National Academy of Sciences USA, 95*, 811–817.
Tyler, C., Chan, H., Liu, L., McBride, B., & Kontsevich, L., (1992). Bit-stealing: How to get 1786 or more grey levels from an 8-bit color monitor. In Rogowitz, B. (Ed.), SPIE Proceedings: Human vision, visual processing, and digital display III. Vol. 1666. pp. 351–364.
Wang, Y., Zhou, Y., Ma, Y., & Leventhal, A. (2005). Degradation of signal timing in cortical areas V1 and V2 of senescent monkeys. *Cerebral Cortex, 15*, 403–408.
Watson, A. B., & Pelli, D. G. (1983). Quest: A bayesian adaptive psychophysical method. *Perception & Psychophysics, 33*, 113–120.
Weale, R. A. (1961). Retinal illumination and age. *Transactions of the Illuminating Engineering Society, 26*, 95–100.